THE PALEOECOLOGY OF THE ORNITHOPOD DINOSAUR *TENONTOSAURUS TILLETTI* FROM THE CLOVERLY FORMATION, BIG HORN BASIN OF WYOMING AND MONTANA

Catherine A. Forster

Department of Geology, University of Pennsylvania
Philadelphia, Pennsylvania 19104

Abstract

Tenontosaurus tilletti, a moderate-sized ornithopod dinosaur, was the major faunal constituent in the early Cretaceous (Aptian-Albian) Cloverly Formation, which crops out around the perimeter of the Big Horn Basin area of south-central Montana and northwestern Wyoming. Paleosols which comprise the *Tenontosaurus*-bearing units of the Cloverly Formation indicate a warm, seasonal climate with a notable increase in the amount of rainfall through time. The flora that was available for consumption by *Tenontosaurus* was primarily gymnospermous but also included some of the earliest angiosperms. Fauna associated with *Tenontosaurus* include fish, turtles, crocodiles, dinosaurs (ankylosaurs, titanosaurs, small- to moderate-sized theropods and ornithopods) and mammals. The major predator of *Tenontosaurus* was the small dromaeosaurid dinosaur *Deinonychus antirrhopus*.

Introduction

Tenontosaurus is a moderate-sized, bipedal ornithopod whose name (meaning "sinew lizard") is derived from a series of ossified tendons which run longitudinally down the neural spines, centra and chevrons of the back and tail. *Tenontosaurus* is the most commonly found vertebrate in the Cloverly Formation and was a major constituent of a Lower Cretaceous community that included dinosaurs (ankylosaurs, sauropods, coelurosaurs, ornithomimids, hypsilophodontids, dromaeosaurs), turtles, crocodiles, and triconodontids (Ostrom, 1970; Sues, 1980). *Tenontosaurus* has been assigned to the family Iguanodontidae by Ostrom (1970), although this classification has been challenged by other authors who believe that *Tenontosaurus* may actually be a member of the family Hypsilophodontidae (Dodson, 1980; Weishampel & Weishampel, 1983).

The *Tenontosaurus*-bearing beds of the Cloverly Formation crop out around the perimeter of the Big Horn Basin in Park, Big Horn, Washakie, and Hot Springs counties in northwestern Wyoming and in Carbon, Wheatland, Big Horn, and Yellowstone counties in south-central Montana. The Cloverly Formation measures up to 200 meters in thickness and is characterized by variegated claystones with numerous sandstone and conglomeratic sandstone facies. It lies unconformably above the non-marine late Jurassic Morrison Formation and is overlain by the Cretaceous Sykes Mountain Formation.

The first *Tenontosaurus* specimen was collected in Big Horn County, Montana, in 1903 by a party from the American Museum of Natural History. Subsequent American Museum expeditions to Montana in 1931, 1932, 1933, and 1938, led by Barnum Brown and Roland T. Bird, uncovered the remains of 18 more individuals. Four more specimens of *Tenontosaurus* were recovered from the Big Horn

---

The Mosasaur, 2:151-163
© 1984 Delaware Valley Paleontological Society

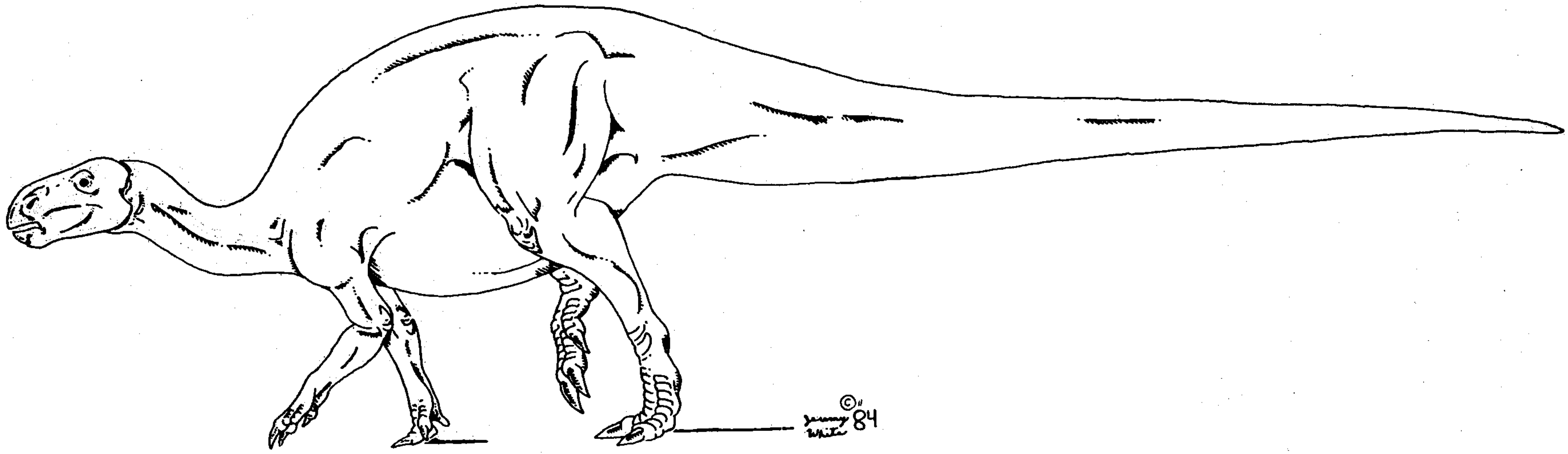

Figure 1. Reconstruction of *Tenontosaurus tilletti*. Drawing by Jeremy White.

Basin the following decade; the University of Oklahoma collected two in 1940; and Al Silberling, a private collector, unearthed two specimens for Princeton University in 1948 and 1949. None of these specimens were described or formally published, although Barnum Brown informally gave the dinosaur the name "Tenantosaurus". In 1962, John H. Ostrom of Yale University began five years of extensive excavation in the Big Horn Basin of Wyoming and Montana. The fauna collected by Yale University included the remains of more than 40 *Tenontosaurus* individuals. In 1970, Ostrom published the first formal description of the genus and species. Field parties from the Museum of Comparative Zoology at Harvard University collected further remains of *Tenontosaurus* from the Big Horn Basin during the mid-1970s.

Since Ostrom's 1970 publication, a number of *Tenontosaurus* remains have been reported from areas other than the Big Horn Basin. These include the Antler Sands (late Aptian-middle Albian) of Oklahoma, the Paluxy Formation (early-middle Albian) of Texas, the Wayan Group (Albian) of Idaho, the Cedar Mountain Formation (Aptian) of Utah, the Arundel Formation (Hautervian-Barremian) of Maryland, and an unnamed unit of Aptian-Albian age in Arizona (Langston, 1974; Galton & Jensen, 1979; Weishampel & Weishampel, 1983). In addition to the extensive skeletal material, one of the Texas specimens was found associated with small patches of skin impressions (Langston, 1974).

All of the skeletal material from the Cloverly Formation in the Big Horn Basin has been identified as *Tenontosaurus tilletti*. Langston (1974), in discussing the Texas and Oklahoma *Tenontosaurus* specimens, cites a number of distinctions between this material and the Cloverly material described by Ostrom in 1970, indicating that these peripheral *Tenontosaurus* populations may be a separate, as yet unnamed species.

To answer the question of the number of *Tenontosaurus* species, as well as that of the familial assignments (mentioned earlier in this paper), *Tenontosaurus* must be thoroughly studied osteologically (this is currently underway, Forster in progress). In addition, *Tenontosaurus* can also be examined in ecological terms; that is, in the context of its environment. Paleoenvironmental information can be obtained from a study of the stratigraphy, sedimentology, and depositional environments of the Cloverly Formation. By studying the paleoenvironment, flora and fauna of the Cloverly Formation *Tenontosaurus* can be viewed not only as a genus of dinosaur, but as a component of a biological system.

Cloverly Formation--
Stratigraphy and Sedimentology

The Cloverly Formation, as redefined by Moberly (1960), consists of three members: the Pryor Conglomerate, the Little Sheep Mudstones, and the Himes Member. These members correspond to Ostrom's Unit IV, Unit V, and Units VI and VII, respectively (Ostrom, 1970). *Tenontosaurus* material has been collected from both the Little Sheep Mudstone Member (Unit V) and the Himes Member (Units VI and VII). To gain some insight into the environment in which *Tenontosaurus* lived, a closer look at the geology of these three members is necessary.

PRYOR CONGLOMERATE. The Pryor Conglomerate is a distinctive, resistant, often lenticular conglomerate and conglomeritic sandstone unit that forms the basal member of the Cloverly Formation throughout much of the Big Horn Basin. It forms a continuous unit, up to 15 meters thick, in the area of the Pryor Mountains in the northernmost Big Horn Basin and thins southeastward to a feather edge around Sykes Mountain. In the central and southern margins of the basin, the Pryor Conglomerate exhibits a sharp, unconformable, erosional contact with the underlying Morrison Formation.

The Pryor Conglomerate is composed of several related lithologies including coarse sandstones, pebbly sandstones, and conglomerates. The unit in the northern Big Horn Basin consists of well-rounded, dark-colored chert grains of all size gradations mixed in varying proportions with angular, light-colored, sand and grit-sized chert and quartz, and sandstone blocks (Moberly, 1960; Ostrom, 1970). As the unit thins towards the southeast the dark, rounded, coarse chert component disappears. South of Sykes Mountain the Pryor Conglomerate appears as a well-sorted quartz arenite interfingering with the lower Little Sheep Mudstone Member. Clay matrix is lacking or minor and consists of kaolinite when present (Lammers, 1939; Moberly, 1960; Ostrom, 1970).

No *Tenontosaurus* remains have been recovered from the Pryor Conglomerate. Whether this is due to the generally coarse nature of the Pryor Conglomerate, which does not lend itself to good fossil preservation, or to the absence of *Tenontosaurus* in the area at the time of the Pryor Conglomerate's deposition, is unknown. An examination of the distribution of *Tenontosaurus* in the overlying Little Sheep Mudstone shows that all of the remains in that unit are found in the upper 12 meters. From this, it is conceivable that *Tenontosaurus* was not present in the area at the time of the deposition of the Pryor Conglomerate.

LITTLE SHEEP MUDSTONE. The Little Sheep Mudstone Member is a persistent, predominantly unstratified series of variegated bentonitic mudstones occasionally containing conglomeritic sandstone lenses. The entire sequence varies in thickness from 5 to 60 meters and overlies the Pryor Conglomerate where present or sits directly on the Morrison Formation.

This unit consists primarily of claystones to very silty mudstones and is highly bentonitic, particularly in the upper part. Bedding is generally absent even on fresh surfaces. The unit is commonly shades of drab gray but is occasionally vividly colored in shades of purple, olive, and

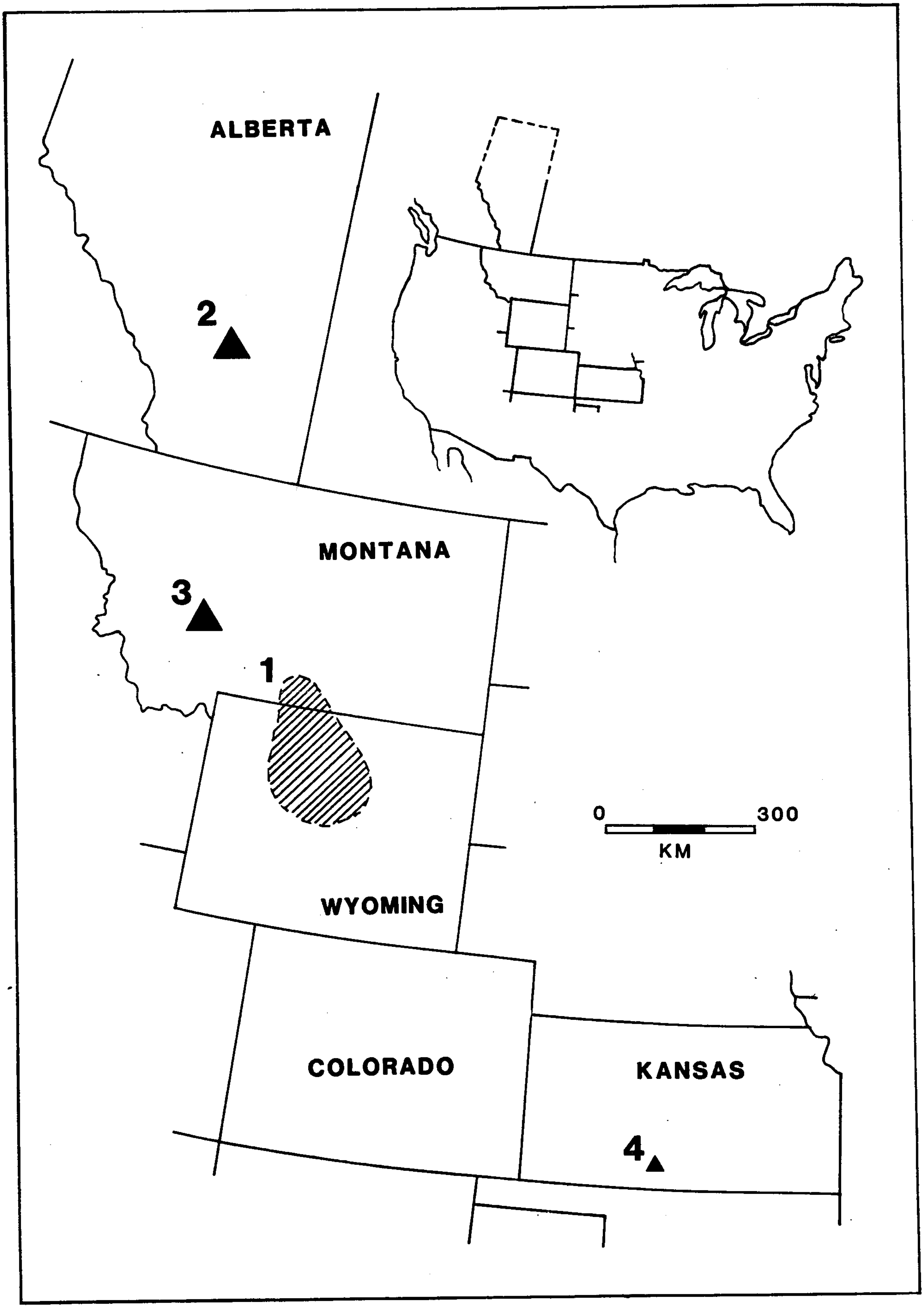

Figure 2. Locations of the Cloverly fauna (1) and related floras: Blairmore (2), Kootenai (3), and Cheyenne (4).

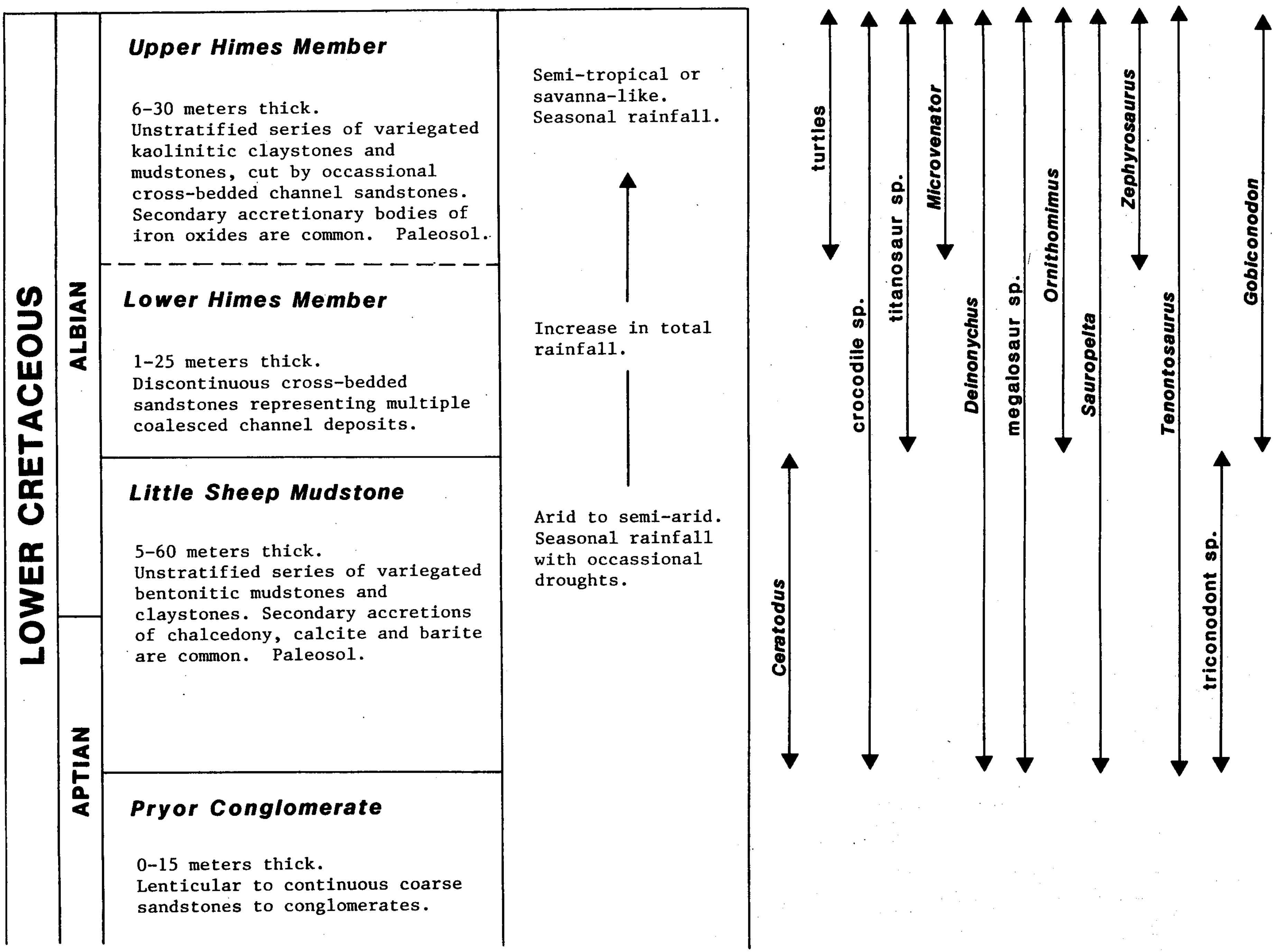
LOWER CRETACEOUS
ALBIAN
APTIAN
Upper Himes Member
6-30 meters thick.
Unstratified series of variegated kaolinitic claystones and mudstones, cut by occassional cross-bedded channel sandstones. Secondary accretionary bodies of iron oxides are common. Paleosol.
Lower Himes Member
1-25 meters thick.
Discontinuous cross-bedded sandstones representing multiple coalesced channel deposits.
Little Sheep Mudstone
5-60 meters thick.
Unstratified series of variegated bentonitic mudstones and claystones. Secondary accretions of chalcedony, calcite and barite are common. Paleosol.
Pryor Conglomerate
0-15 meters thick.
Lenticular to continuous coarse sandstones to conglomerates.
Semi-tropical or savanna-like. Seasonal rainfall.
Increase in total rainfall.
Arid to semi-arid. Seasonal rainfall with occassional droughts.
Ceratodus
turtles
crocodile sp.
titanosaur sp.
Microvenator
Deinonychus
megalosaur sp.
Ornithomimus
Sauropelta
Zephyrosaurus
Tenontosaurus
triconodont sp.
Gobiconodon

Figure 3. Stratigraphy, paleoenvironment, and faunal distribution within the Cloverly Formation.

dusky to pale red. Color changes occur independently of bedding, jointing, and other structures (Moberly, 1962; Ostrom, 1970). When moistened, the bentonitic mudstones undergo rapid color changes, swell, and disintegrate. This weathering characteristic results in low, rounded "gumbo" hills that are devoid of vegetation (Moberly, 1962; Ostrom, 1970).

Nodules and nodular layers of chalcedony, barite, and calcite occur throughout the unit. Selenite crystals, satin spar veins, petrified wood, and septarian nodules are locally abundant. Clean quartz sandstones, white limestones, silicified tuffs, and chert beds, ranging up to one meter in thickness, also occur in the unit (Peck & Reker, 1948; Moberly, 1960, 1962; Ostrom, 1970).

Of the 69 stratigraphically located *Tenontosaurus* individuals that have been recovered within the Big Horn Basin (this number includes not only the two dozen partial to complete skeletons but any fragmentary or isolated material attributed to *Tenontosaurus*), 23 (30 percent) have come from the Little Sheep Mudstone. These may represent the initial *Tenontosaurus* population in the Big Horn Basin.

HIMES MEMBER. The Himes Member consists of variegated claystones, sandstone beds, and lenticular sandstones. It is divided into an upper unit and a lower unit and represents the uppermost member of the Cloverly Formation.

The lower unit of the Himes Member is a lenticular, discontinuous, cross-bedded, and usually coarse-grained sandstone that locally cuts into the underlying Little Sheep Mudstone Member. Where channeling does not occur, the boundary is marked by an irregular but sharp disconformity (Moberly, 1960; Ostrom, 1970). The sands of the lower unit are discontinuous and represent multiple coalesced channel deposits rather than a single, continuous depositional sequence.

The lower unit consists of olive-gray, yellow, or brown sandstones having a "salt-and-pepper" aspect resulting from its admixture of lithic grains and partially decomposed feldspars in a montmorillonitic matrix (Moberly, 1960; Ostrom, 1970). The sand grains are angular to sub-angular and consist mainly of quartz and feldspar. Large fragments of gray or yellow chert and light-colored quartzite are found in the northern part of the basin, while fragments of white chert are found mixed in the sandstones in the southern part. Where the sandstones are well-indurated, they form massive, resistant ledges, although they are more commonly friable and disintegrate readily (Ostrom, 1970). These sandstone lenses grade upward into the sandy mudstones and then claystones of the upper unit of the Himes Member.

Only four specimens of *Tenontosaurus* have come from the lower Himes Member. These remains occurred as isolated and water-worn fragments (Ostrom, 1970). No articulated or semi-articulated specimens of any species have been found in the lower Himes Member.

The brightly colored, variegated claystones of the upper Himes Member are the most persistent and prominent facies of the Cloverly Formation. This sequence ranges from 6 to 30 meters in thickness and weathers into steep fluted cliffs or slopes and occasionally into badlands.

The upper unit consists of maroon, red, orange, deep purple, yellow, and red-brown kaolinitic mudstones that most commonly lack bedding. The mudstones are locally sandy and occasionally calcareous or bentonitic (Ostrom, 1970). Nodular limestone beds over one meter thick have been reported in some parts of the upper Himes Member (Peck & Reker, 1948). The claystones and mudstones of the Himes Member are generally finer-grained than those of the Little Sheep Mudstone and contain abundant secondary accretionary bodies of iron oxides in veinlets, patches, and well-indurated layers. Occasional concentrations of chalcedony concretions and satin spar also occur (Moberly, 1960; Ostrom, 1970). The mudstones are frequently dissected by elongate, cross-bedded sandstone bodies that have been interpreted as channel deposits (Moberly, 1960, 1962; Ostrom, 1970).

Forty-four *Tenontosaurus* specimens (64 percent of the recovered material) have come from the upper Himes Member. Several factors may contribute to the apparent preponderance of *Tenontosaurus* in this unit: 1) there may have been more of them at that time; 2) the upper Himes Member is the most fossiliferous bed and as a result the most heavily collected, injecting a "collector's bias" into the numbers; and 3) the abundance of fossils in this unit relative to the rest of the Cloverly Formation may be an artifact of better preservation within the upper unit.

Sediment Sources, Deposition, and Diagenesis

The Cloverly Formation forms the base of a thick sedimentary wedge that was deposited east of the Sevier orogenic belt. This early Cretaceous uplift was the major source of clastic sediments to a large north-south trending foreland basin which included most of Wyoming and parts of Montana throughout the Cretaceous.

TECTONIC HISTORY. The development of this foreland basin in the interior of the Western United States is linked to the overall geodynamics of an active continental margin. The continental rearrangement, which began in the late Triassic and early Jurassic with the break-up of Pangea and the opening of the Atlantic Ocean, continued throughout the Cretaceous. By late Jurassic and early Cretaceous time, the plate carrying North America was overriding the oceanic Farallon plate from Alaska southward (Coney, 1977; Dickinson, 1976). This newly developed arc-trench system formed an extensive series of north-south trending backarc fold-thrust belts with a retroarc foreland basin along their eastern margins. This thrusting event, termed the Sevier Orogeny, shed large amounts of detritus that accumulated as thick deposits in the foreland basin during the early Cretaceous (Armstrong, 1968; Armstrong & Oriel, 1965; Dickinson, 1976; Jordan, 1981).

Uplift along the Idaho-Wyoming portion of the thrust belt provided the bulk of the clastic debris deposited in the Big Horn Basin region of Wyoming (Jordan, 1981; Moberly, 1962; Young, 1970). The Pryor Conglomerate Member of the Cloverly Formation is a synorogenic conglomerate which represents sediment input from the initial deformation along the thrust belt. This initial deformation, the Paris Thrust, continued its activity throughout the deposition of the Cloverly Formation (Jordan, 1981).

PALEOCURRENTS. Paleocurrents in the Cloverly Formation can be examined to infer drainage patterns and source areas for the sediments. Cross bedding and channel trends in the Pryor Conglomerate show a dominant current direction from the west and northwest, with the most persistent trends occurring in the coarser beds in the northern Big Horn Basin. Some of the finer beds in the southern part of the basin were transported from the east (Moberly, 1960, 1962). These conglomeritic sandstones often appear as braided channels (Moberly, 1960; MacKenzie & Ryan, 1962). No current directions have been obtained from the mudstones of the Little Sheep Member. The sandstones of the lower Himes Member, like the Pryor Conglomerate, show a general current flow from the west and northwest (Moberly, 1960). The elongate channel sandstones which cut through the claystones of the upper Himes Member show the dominant current direction to be from the northeast, with two of the major rivers flowing from the east (Moberly, 1960).

PROVENANCE. The paleocurrent directions, tectonic setting, and mineral analyses of the Cloverly Formation can be integrated to postulate the following depositional sequence.

1. Sediments comprising the Pryor Conglomerate, Little Sheep Mudstone, and the lower Himes Member were transported into the Big Horn Basin from the upthrust highlands to the west and northwest in Idaho and westernmost Wyoming.

2. Channel sands in the upper Himes Member were transported from the east and northeast and consequently exhibit a different heavy mineral suite than the rest of the Cloverly Formation (Moberly, 1960; Mirsky, 1962). Uplifting in the Black Hills region of South Dakota and eastern Wyoming is the probable sediment source for the channel sands in the upper Himes Member (Crowley, 1951; Moberly, 1960, 1962; MacKenzie & Ryan, 1962).

3. Volcanic input contributed a significant amount of sediment to the Cloverly Formation. Lithic fragments in the lower Himes Member, tuff and lava fragments, pumice ash, lapilli, silicified tuffs, and the abundance of montmorillonitic clays and bentonite beds in various parts of the formation are all of volcanic origin. Airborne ash from volcanic eruptions in the Nevadan orogenic arc and the transportation into the basin of debris derived from volcanic materials have been suggested as sources of these sediments (Moberly, 1960; MacKenzie & Ryan, 1962).

PALEOSOLS. The mudstones of the Little Sheep Mudstone and the upper Himes Member have been interpreted as fossilized soil horizons developed on a broad area of low relief and elevation (Moberly, 1960, 1962). Features present in the mudstones themselves are similar to those found in recently forming soils. Although some *Tenontosaurus* material is recovered from the lower unit of the Himes Member, the bulk of the *Tenontosaurus* remains have been found in the fine-grained claystones of the Little Sheep Mudstone and the upper Himes Member. The only articulated skeletons are found in the mudstones, particularly in the gray mudstones (Ostrom, 1970; Dodson *et al.*, 1980a). Bown & Kraus (1981), in their work on the paleosols of the Willwood Formation, have also noticed a tendancy for most vertebrate fossils to be found in a gray rather than brightly colored, more oxidized, claystones.

Bentonite and montmorillonite, the major components of the Little Sheep Mudstone, form as a result of weathering of volcanic ash in either arid regions or those with pronounced dry seasons (Brady, 1974; Battey, 1978; Buol *et al.*, 1980). There is ample evidence for a volcanic origin for much of the Little Sheep Mudstone, including relic volcanic textures in mineral grains, tuff and lava fragments, feldspar and biotite euhedra, pumice ash, lapilli, and silicified tuffs (Moberly, 1960, 1962; Ostrom, 1970). This indicates that the climate at the time of deposition was arid and/or had a wet-dry seasonality.

The secondary deposits of nodules and layers of calcium carbonates in the Little Sheep Mudstone are indicative of soils in arid or semi-arid climates which experience a fairly minimal amount of rainfall. In these climates enough water is present to dissolve the minerals and relocate them within the soil profile, but moisture is still not present in sufficient quantities to remove them completely. In wetter climates calcium carbonates are flushed from the soil and are not redeposited within the profile (Buol *et al.*, 1980; Retallack, 1983). To precipitate these dissolved carbonates into a calcic horizon, the soil must be periodically "dried out," again indicating a wet-dry seasonality during the Little Sheep Mudstone's development.

The ubiquitous chalcedony nodules and layers in the Little Sheep Mudstone are common in fairly unleached soils and are often found in association with calcium carbonate deposits in dry regions (Battey, 1978; Buol *et al.*; Retallack, 1983). Retallack (1983) states that petrocalcic horizons and chalcedony pseudomorphs of barite are indicative of soils that have experienced severe drought conditions. Chalcedony-barite nodules are common in the Little Sheep Mudstone, as are nodules of pure chalcedony and pure barite (Ostrom, 1970).

The paleosols of the Little Sheep Mudstone indicate an arid to semi-arid climate, low rainfall, and a wet-dry seasonality marked by occasional droughts at their time of deformation. The resulting low levels of leaching left high concentrations of silica, calcium carbonates, and magnesium in the soils which were mobilized within the soil during wet conditions and redeposited in layers and patches in the drier seasons. This same weathering regime, acting on the large volume of volcanic input into the system, produced bentonitic and montmorillonitic clays.

The upper unit of the Himes Member appears to have formed under different conditions than the Little Sheep Mudstone. The dominant clay in the upper Himes Member is kaolinite. Kaolinite, a 1:1 clay, forms from the decomposition of 2:1 (montmorillonite-type clays), and 2:2 clays through either intense weathering or extended times of exposure (Sherman, 1951; Weaver, 1973; Brady, 1974). Brady (1974) claims that kaolinite dominates soils only under tropical or semi-tropical conditions where intense weathering has removed most of the silica. The decomposition of silicates under this intense weathering results in an absence in the soil of calcareous and siliceous deposits. These types of secondary deposits, while common in the Little Sheep Mudstone, are rare in the Himes Member.

The common secondary accretions in the upper Himes Member are iron oxides in veinlets, irregular patches, nodules and well-indurated hardpans. Only occasional calcareous layers and chalcedony nodules have been reported (Peck & Reker, 1948; Moberly, 1960; Ostrom, 1970). This accumulation of iron oxides in soil horizons is linked to the desilicification of the profile through leaching. Since aluminum (which is tied up in the kaolinite crystal lattice) and iron are the last elements to be leached from a soil, their relative abundance demonstrates that the bulk of the calcium, magnesium, and silica has been mobilized and removed from the profile. Iron oxides and well-indurated hardpans or ironstones accumulate in areas that have a fluctuating water table near the soil surface which translocates and redeposits the iron within the profile. Iron is hydrated in the presence of moisture and redeposited at depth when the soil dries out. If subjected to continuous wetting and drying, small accumulations of iron oxides become indurated into thick layers or beds of irregular nodular aggregates (Sherman, 1951; Prescott & Pendleton, 1952; Ollier, 1967; MacFarlane, 1976; Buol *et al.*, 1980).

Color mottling is also related to this alternating wetting and drying of the soil, which sets up local reducing (wet) conditions to put the iron into solution. When the soil dries the iron is redeposited in irregular patches, or mottles, in the soil profile (Buol *et al.*, 1980; Bown & Kraus, 1981). Mottling is common in the upper Himes Member (Moberly, 1962; Ostrom, 1970). This wet-dry seasonality is crucial for the deposition of iron oxide layers within the soil horizon. In climates with wet and dry seasons, the iron oxides become stabilized while the pedogenic weathering causes the loss of silica and aluminum. Iron oxides are hydrated and dehydrated during wet and dry periods which favor their accumulation in the soil horizon. Under conditions of higher rainfall or continuous wet climates, free oxides of aluminum become the dominant oxides (Sherman, 1951; Prescott & Pendleton, 1952; MacFarlane, 1976). Warm temperatures, which aid desilicification, also favor the development of soils rich in iron oxides (MacFarlane, 1976). The tendency towards bright colors in the unit, particularly the purples, pinks, and reds, mirror the highly oxidized nature of these paleosols.

Moberly (1960, 1962) suggests a savannah-type climate with a moderately high rainfall and a marked dry season as the paleoclimate for the Cloverly Formation. This seems satisfactory for only the upper Himes Member, as the Little Sheep Mudstone appears to have developed under much drier conditions. The major climatic change from Little Sheep Mudstone times to those of the upper Himes Member is a marked increase in total rainfall, while warm temperatures and a wet-dry seasonality remained a constant environmental feature.

Environmental Conclusions

Tenontosaurus appears to have been an adaptable animal, persisting in one geographic area over not only a long temporal span but through marked climatic changes as well. The *Tenontosaurus* of the drought-prone, semi-arid Little Sheep Mudstone times successfully made the transition into and through the more humid, sub-tropical early Albian.

The apparent increase in rainfall from the Little Sheep Mudstone to the upper Himes Member, reflected in the sedimentology of the paleosols, appears to be part of a trend toward increasing precipitation as evidenced by the overlying strata. Directly above the upper Himes Member is the Sykes Mountain Formation, which grades upward into the marine Thermopolis Shale. The Sykes Mountain Formation (the Greybull Sandstone and "Rusty Beds" of some authors) consists of sandstones and interbedded siltstones and shales containing abundant ripple marks and fucoidal impressions. These have been interpreted as tidal and mudflat deposits laid down around the perimeter of the transgressing Skull Creek Seaway (Moberly, 1960, 1962; Ostrom, 1970). This embayment from the Arctic Ocean deposited the black, fissile Thermopolis Shale over the Big Horn Basin area during the mid-Albian (McGookey, 1972). As this seaway transgressed southward through the center of North America in the early Albian, the Big Horn Basin area approached sea level and attained a more coastal climatic regime. This probably accounts for the increase in rainfall from the Little Sheep Mudstone to the upper Himes Member.

Seventy percent of all *Tenontosaurus* material has been recovered from the upper Himes Member.

As mentioned earlier, there are a number of reasons for this increase including collecting biases and preferential preservation within the upper Himes Member. However, the change from the drier Little Sheep Mudstone environment to that of the more humid, increasingly coastal upper Himes Member was probably accompanied by a more diverse and abundant biological community. Ostrom (1970) reports that the upper Himes Member is the most fossiliferous member of the Cloverly Formation. If this is due to increased biological production in the upper Himes Member, then the increase in abundance of *Tenontosaurus* is real and not merely an artifact of better preservation.

To explore the question of faunal and floral diversity throughout the Cloverly Formation one must look at the fossils themselves. With the depositional, paleogeographic, and paleoclimatologic data as a backdrop the paleobiological information will now be examined.

Floral and Faunal Analyses

RELATED FLORAS. No megafloral or palynological assemblages have been described from the Cloverly Formation. Since there is no direct evidence, floras from surrounding time-equivalent formations must be examined for an approximation of the plant life in the Cloverly. While this approach is not necessarily accurate, nor can it give any information on floral changes between members, it represents the "best guess" until careful paleobotanic work is done on the Cloverly Formation.

Floral assemblages have been described from a handful of early Cretaceous formations of North America, including the Cheyenne Sandstone of western Kansas, the Kootenai Formation of central and southwestern Montana, and the lower Blairmore Group of southern Alberta. These three formations seem appropriate for comparison for the following reasons: 1) their floras are fairly extensive and well-known, 2) they geographically surround the Big Horn Basin, and 3) they are syndepositional with the Cloverly Formation. The Kootenai Formation in Montana is late Aptian-early Albian in age (Cobban & Reeside, 1952; MacKenzie & Ryan, 1962; Ostrom, 1970). The Cheyenne Sandstone is considered to be late Aptian-early Albian by most workers (Cobban & Reeside, 1952; MacKenzie & Ryan, 1962; Young, 1970; Ostrom, 1970), although Bell (1956) places it entirely within the early Albian. The base of the Blairmore Group, where the lower flora is found, has similarly been assigned to the late Aptian-early Albian by some (Cobban & Reeside, 1952; Bell, 1956), and to the early Albian by Singh (1975).

These three formations contain primarily gymnospermous floras rich in ferns, seed ferns, conifers, cycads, and gingkos. Angiosperms are relatively abundant in the Cheyenne Sandstone, contrasting with the lower Blairmore Group which contains only a single angiosperm, *Sapindopsis*, and the Kootenai Formation where no angiosperms have been reported (see Table 1).

Table 1. Distribution of flora within the Cheyenne and Kootenai Formations and lower Blairmore Group[1]

	Cheyenne	Kootenai	Blairmore
Pteridophyta			
Acrostichopteris		x	
Cladophlebis	x	x	x
Coniopteris		x	
Dryopteris		x	
Gleicheneites	x		
Klukia			x
Onychopsis		x	
Pteridospermophyta			
Caytonia			x
Hydropterangium			x
Sagenopteris		x	
Pteridophyta/Pteridospermophyta			
Sphenopteris	x	x	x
Cycadophyta			
Ctenopteris			x
"Cycadospermum"	x	x	
Nilssonia		x	x
Pterophyllum		x	
Ptilophyllum		x	x
Pseudocycas			x
Zamites			x
Coniferophyta			
"Abietites"	x		
Athrotaxites		x	x
Cupressinoxylon	x		
Czekanowskia		x	
Alatides			x
Elatocladus			x
"Laricopsis"		x	
Nageiopsis		x	x
Pagiophyllum			x
Pityophyllum		x	x
Podozamites		x	x
Sequoia	x	x	
Ginkopdyta			
Baiera		x	
Carpolithus		x	
Gingko		x	x
Phoenicopsis			x
Sphenophyta			
Equisetum		x	
Equisitites			x
Angiospermophyta			
Aralia	x		
Araliopsoides	x		
"Arundo"	x		
Sapindopsis	x		x
"Sassafras"	x		
"Sterculia"	x		
Miscellaneous			
Thallites			x

---

[1] Fontaine (1905), Ward (1905), Knowlton (1907), Fisher (1909), Berry (1921), Bell (1956)

Any one or more of several factors may account for the variability in angiosperm abundance between the floras:

1. The Cheyenne Sandstone may be slightly younger than the Kootenai Formation and the lower Blairmore Group.

2. Cretaceous angiosperms appear in progressively younger rocks at higher latitudes, implying their migration from the lower latitudes poleward (Axelrod, 1970; Hughes, 1977). Since the Cheyenne Sandstone was deposited at a lower paleolatitude than either the Kootenai Formation or the lower Blairmore Group, angiosperms reached the area that is now Kansas prior to spreading into Montana and Alberta.

3. The exact stratigraphic position of the three floras, and thus the exact time interval they represent, is unknown.

The Cheyenne, Kootenai, and lower Blairmore floras share the same major plant groups but exhibit differences on the generic level. Only the two form-genera, *Cladophlebis* and *Sphenopteris*, are common to all three assemblages. The Cheyenne and Kootenai floras also share the genera *Sequoia* and "*Cycadospermum*", while the angiosperm *Sapindopsis* is the only other genus common to both the Cheyenne and the lower Blairmore floras. There is a much greater taxonomic similarity between the lower Blairmore and Kootenai floras which both contain *Coniopteris, Sagenopteris, Nilssonia, Ptilophyllum, Athrotaxites, Nageiopsis, Pityophyllum, Podozamites,* and *Gingko.*

Of these three assemblages, the Kootenai flora offers the closest approximation to that of the Cloverly Formation due to their geographic proximity and close time correlation. The Kootenai Formation occurs adjacent to the Big Horn Basin in central and southwestern Montana and is lithologically equivalent to the Cloverly Formation. Like the Cloverly Formation, it lies unconformably over the upper Jurassic Morrison Formation and has synorogenic sandstones and conglomeratic sandstones at its base (Bauer & Robinson, 1923; Lammers, 1939; Cobban & Reeside, 1952; Haun & Barlow, 1962).

Cobban & Reeside (1952) place both the Cloverly Formation and the Kootenai Formation within a faunal zone marked by the freshwater mollusc *Protelliptio douglassi*, in association with *Unio farri* and "*Campeloma harlowtonensis*". A distinctive charophyte oogonia and ostracode assemblage, including *Cypridea inornata, C. wyomingensis, C. anomala,* and *Theriosynoecum angularis,* "*Atopochara trivolvis*", and "*Flabellochara harrisi*", appear in both the Kootenai and the Cloverly Formations (Peck & Reker, 1948; Yen, 1949; Peck, 1951; Cobban & Reeside, 1952; Peck & Craig, 1962). Moberly (1960) also reports the presence of the freshwater gastropod "*Reesidella montanaensis*" in limestone beds from both the Kootenai Formation and the Little Sheep Mudstone Member of the Cloverly Formation. This clearly demonstrates the close temporal relationship between the two formations.

On the basis of these three floral assemblages one can postulate with some confidence a predominantly gymnospermous community consisting of conifers, cycads and gingkos, and ferns and tree ferns for the Cloverly Formation. Although early angiosperms such as *Sapindopsis* have not been reported from the Kootenai Formation, their presence in both the lower Blairmore and Cheyenne floras indicates that angiosperms probably formed a small part of the Kootenai flora as well. Therefore, while gymnosperms still comprised the bulk of the plant community, early angiosperms had probably infilatrated the Big Horn Basin area by the close of Cloverly times.

As an herbivore, *Tenontosaurus* is linked to the flora in the Cloverly Formation and indeed seems well equipped to have dealt with it. The premaxilla and predentary of *Tenontosaurus* flare out into a broad, U-shaped, toothless beak that was probably capped by a horny bill in life. Directly behind this beak in the maxillae and dentaries are rows of 10 to 13 unilaterally enameled cheek teeth. Buccally enameled maxillary teeth oppose lingually enameled dentary teeth, resulting in self-sharpening teeth with wear surfaces which are medially inclined 45 degrees to 60 degrees from horizontal (Weishampel, 1981). The teeth themselves are laterally compressed but broad with denticulate margins. As these teeth were ground down through wear they were replaced by new teeth.

The jaws of *Tenontosaurus* are capable of vertical crushing motions and lateral movement, the latter due to a transverse "power stroke" between the maxillary and dentary teeth. In this power stroke, the maxillae are forced to splay laterally when they contact the dentary teeth. This results in a transverse tearing and cutting motion as the upper and lower teeth shear past each other (Weishampel, 1981).

The major dietary restriction on *Tenontosaurus* appears to have been that it was at best a low to moderate browser. A large adult *Tenontosaurus* could crop food to a maximum height of about three meters in a bipedal stance. This restricted *Tenontosaurus*, particularly the younger individuals, to plants that could be reached at fairly low levels; that is, to small- or moderate-sized plant species and submature individuals of the larger plant species. Leaves, wood, and fructifications may have all formed part of *Tenontosaurus*'s diet.

FAUNA. Compared to the paucity of floral information in the Cloverly Formation, much is known about the fauna. A fairly extensive and diverse vertebrate assemblage has been collected from the Cloverly Formation.

The Cloverly Formation contains a distinctive fauna that differs significantly from the fauna of the underlying Morrison Formation. The Morrison fauna was replaced by a community characterized by species of much smaller size by Cloverly times. Because of the long depositional hiatus between the two formations, the time, mode, and reason for the changeover from one fauna to the other is unknown. Extinction, migration, and environmental and climatic changes may have all played roles.

The Cloverly fauna includes bony fish, lung fish, turtles, crocodiles, ankylosaurs, titanosaurs, small- to moderate-sized theropods and ornithopods, and mammals. The distribution of the Cloverly fauna is summarized in Table 2.

Table 2. Known fauna from the Cloverly Formation[1]

	Member		
Fauna	Little Sheep	lower Himes	upper Himes
Order Amiiformes			
F. ?			
amioid indet.			x
Order Dipnoi			
F. Ceratodontidae			
Ceratodus frazieri	x		
F. ?			
dipnoan indet.			x
Order Testudinata			
F. Glyptopsidae			
Naomichelys speciosa			x
Glyptops pervicax			x
F. Testudinidae			
testudinid indet.			x
Order Crocodilia			
F. Goniopholidae			
crocodile indet.	x	x	x
Order Saurischia			
F. Titanosauridae			
titanosaurid indet.		x	x
F. Coeluridae			
Microvenator celer			x
F. Dromaeosauridae			
Deinonychus antirrhopus	x		x
F. Megalosauridae			
megalosaurid indet.	x	x	x
F. Ornithomimidae			
Ornithomimus sp.		x	x
Order Ornithischia			
F. Acanthopholidae			
Sauropelta edwardsi	x	x	x
F. Hypsilophodontidae			
Zephrosaurus schaffi			x
F. Iguanodontidae			
Tenontosaurus tilletti	x	x	x
Order Triconodontidae			
F. ?			
triconodontid indet.	x		
F. ?			
Gobiconodon sp.		x	x

---

[1] Ostrom (1970), Jenkins & Crompton (1979), Sues (1980), C. Schaff (pers. commun.)

The ranges of nearly all the Cloverly genera either include or lie entirely within the upper Himes Member. Nearly half (47 percent) of the Cloverly fauna exists solely within this uppermost unit. Only the lungfish *Ceratodus frazieri* and the tricodontids (indet.) have not been found in the upper Himes Member; they occur only in the Little Sheep Mudstone. Crocodiles (indet.), magalosaurs (indet.), *Deinonychus*, *Sauropelta*, and *Tenontosaurus* have ranges that span the upper three units of the Cloverly Formation. More individual vertebrate remains have been recovered from the upper Himes Member than from both the Little Sheep Mudstone and the lower Himes Member combined, making the fauna of the upper Himes Member not only the most diverse, but also the most abundant. Owing to the general unfossiliferous nature of the Cloverly Formation, the possibility that the rest of the known taxa also spans the entire Cloverly Formation cannot be excluded.

Absolute numbers of individuals per genus are difficult to tabulate, but relative abundances are easily attained. Ostrom (1970), after examining all of the Cloverly vertebrates, listed their relative frequencies as:

Ornithopods	F. Hypsilophodontidae, F. Iguanodontidae
Ankylosaurs	F. Acanthopholidae
Sauropods	F. Titanosauridae
Theropods	F. Coeluridae, F. Dromaeosauridae, F. Megalosauridae, F. Ornithomimidae
Crocodiles	F. Goniopholidae
Turtles	F. Glyptopsidae, F. Testudinidae

The ornithopods, represented almost exclusively by *Tenontosaurus*, are five times more common than the second most abundant group, the ankylosaurs. The three major herbivorous groups, the ornithopods, ankylosaurs, and sauropods, are the most common with the carnivorous theropods ranking fourth. In abundance, herbivores by far outstrip their predators.

This situation, where the number of prey individuals significantly outweighs that of the predators, differs markedly from that of the underlying Morrison Formation. In the Morrison Formation the major predator, *Allosaurus*, is commonly associated with prey genera at nearly every site (Dodson *et al.*, 1980). At one site, the Cleveland-Lloyd quarry, *Allosaurus* remains outnumber those of herbivores (Farlow, 1976). In terms of predator/prey ratios, the Cloverly Formation more closely resembles later Cretaceous formations, such as the Judith River, where herbivores significantly outnumber carnivores (Dodson, 1983).

Four carnivorous dinosaurs have been found in the Cloverly Formation: *Deinonychus*, *Microvenator*, *Ornithomimus*, and an unidentified megalosaur. *Microvenator*, a lightly built, turkey-sized animal and the larger "ostrich dinosaur" *Ornithomimus* are very rare (two and three recovered, respectively)

(Ostrom, 1970). Both their scarcity and size make them doubtful predators of *Tenontosaurus*. The largest carnivores in the Cloverly fauna were the megalosaurs. Fragmentary remains of only eight of these theropods have been found. While the megalosaurs were certainly large enough to prey on *Tenontosaurus*--and probably did--their relative scarcity again precludes them from playing a major role in *Tenontosaurus* predation. *Tenontosaurus* and megalosaur remains have been found in association at only one site. It is likely that the megalosaurs preyed more frequently on the largest herbivores in the Cloverly fauna, the sauropods. Megalosaurs in fact have been found with sauropod remains at four sites (Ostrom, 1970).

By far the most numerous predator in the Cloverly fauna is the small but dynamic dromaeosaur *Deinonychus antirrhopus*. *Deinonychus* exhibits many features, such as a large skull, long flexible arms, and well-developed hind limbs with a sickle-like claw on each foot, which indicate that this formidable predator was agile, active, and intelligent.

Deinonychus, by virtue of being the most common predator of the Cloverly fauna, is the likely candidate for being the major *Tenontosaurus* predator. This supposition is well supported by the data. *Deinonychus* remains, represented almost exclusively by isolated teeth, have been found in association with *Tenontosaurus* remains at 16 sites in the Cloverly Formation. Nearly 20 percent of all recovered *Tenontosaurus* material has been found with *Deinonychus*, three times the frequency that *Tenontosaurus* is found with any other faunal constituent. Conversely, more than 30 percent of all recovered *Deinonychus* remains have been associated with *Tenontosaurus*, five times the frequency that *Deinonychus* is found with any other prey genus. The frequency in which *Deinonychus* teeth are found with *Tenontosaurus* remains, relative to any other prey animal, seems to indicate a definite preference by *Deinonychus* for *Tenontosaurus*.

Although *Deinonychus* was certainly an active and capable predator, it was a small animal. A full-grown *Tenontosaurus* would be four or five times the size of an adult *Deinonychus*. An adult *Deinonychus* was probably unable, scimitar-like claw notwithstanding, to singlehandedly kill a large *Tenontosaurus*.

Due to this size difference, it is likely that once a *Tentontosaurus* reached a certain size, it passed out of the range of *Deinonychus*'s predatory capabilities and was no longer available as prey. *Deinonychus* would have therefore been limited to younger tenontosaurs. It has also been suggested (Ostrom, 1969; Farlow, 1976) that *Deinonychus* was gregarious and hunted in packs, allowing these small carnivores to prey on larger tentontosaurs than any one of them could have hunted singlehandedly.

An examination of the sizes of the tenontosaurs found associated with *Deinonychus* reveals that the majority were in the half-grown range. A few were either small juveniles or large adults. However, the largest *Tenontosaurus* yet recovered, an American Museum of Natural History specimen, was found associated with *Deinonychus* teeth. It may even be possible that *Deinonychus* was an opportunistic scavenger. The size distribution of tenontosaurs found associated with *Deinonychus* also mimics the overall *Tenontosaurus* size distribution.

Conclusions

Tenontosaurus was a common constituent in a community of generally small- to moderately-sized vertebrates. Its major predator was a small dromaeosaur called *Deinonychus*, as evidenced by the frequent association of *Tenontosaurus* with *Deinonychus* teeth. The temporal distribution of the Cloverly fauna superficially exhibits an increase in diversity and numbers from the Little Sheep Mudstone to the upper Himes Member. Turtles, bony fish, sauropods, *Microvenator*, *Ornithomimus*, and *Zephyrosaurus* appear for the first time in the uppermost unit. The number of individuals per genus also increases dramatically. This increase in numbers of individuals may be due to the more equitable climate during upper Himes times. The increased diversity may also be a result of this climatic shift, although it cannot be proven by the present fossil record. The absence of some genera in the Little Sheep Mudstone may be due not to lack of existence but to lack of discovery.

Acknowledgements

I would like to thank William Gallagher for inviting me to contribute this article to *The Mosasaur*. I would also like to extend my gratitude to the following people who have graciously allowed me access to material in their care: J. Ostrom, C. Schaff, F. Fenkins, Jr., and E. Gaffney. Discussion, guidance, and review of the manuscript throughout its formation was gratefully accepted from P. Dodson, W. Gallagher, D. Baird, and R. Wood. Part of the research for this paper was accomplished through a grant from Sigma Xi.

References Cited

ARMSTRONG, Frank C., & Steven C. ORIEL. 1965. Tectonic development of Idaho-Wyoming thrust belt. *Am. Assoc. Petroleum Geologists Bull.*, 49(11):1847-1866.

ARMSTRONG, Richard Lee. 1968. Sevier Orogenic Belt in Nevada and Utah. *Geol. Soc. America Bull.*, 79:429-458.

AXELROD, Daniel I. 1970. Mesozoic paleogeography and early angiosperm history. *Botanical Review*, 36:277-319.

BATTEY. 1978. *Mineralogy for students*. London: Longman Group, Ltd.

BAUER, C. Max & Ernest Guy ROBINSON. 1923. Comparative stratigraphy in Montana. *Am. Assoc. Petroleum Geologists Bull.*, 7:159-178.

BELL, W. A. 1956. *Lower Cretaceous floras of western Canada.* Geol. Survey Canada Mem. 285, pp. 1-331.

BERRY, Edward Wilbur. 1921. *The flora of the Cheyenne Sandstone of Kansas*. U.S. Geol. Survey Prof. Paper 129, pp. 199-224.

BRADY, Nyle C. 1974. *The nature and properties of soils*. New York: Macmillan Pub. Co.

BOWN, Thomas M. & Mary J. KRAUS. 1981. Lower Eocene alluvial paleosols (Willwood Formation, northwest Wyoming, U.S.A.) and their significance for paleoecology, paleoclimatology, and basin analysis. *Paleogeography, Palaeoclimatology, Paleoecology,* 34:1-30.

BUOL, S. W., F. D. HOLE, & R. J. McCRACKEN. 1980. *Soil genesis and classification.* Ames: Iowa State Univ. Press.

BURK, C. A. 1957. Stratigraphic summary of the nonmarine upper Jurassic and lower Cretaceous strata of Wyoming. *Wyoming Geol. Assoc. Guidebook,* pp. 55-62.

COBBAN, William A. & John B. REESIDE. 1952. Correlation of the Cretaceous formations of the Western Interior of the United States. *Geol. Soc. America Bull.,* 63:1011-1044.

CONEY, Peter J. 1977. Mesozoic-Cenozoic Cordilleran plate tectonics. *Geol. Soc. America Mem. 152,* pp. 33-50.

CROWLEY, A. J. 1951. Possible lower Cretaceous uplifting of Black Hills, Wyoming and South Dakota. *Am. Assoc. Petroleum Geologists Bull.,* 35(1):83-107.

DICKINSON, William R. 1976. Sedimentary basins developed during evolution of Mesozoic-Cenozoic arc-trench system in western North America. *Canadian Jour. Earth Science,* 13:1268-1287.

DODSON, Peter. 1980. Comparative osteology of the American ornithopods *Camptosaurus* and *Tenontosaurus*. *Mem. Soc. Geol. France,* n.s., 139:87-93.

DODSON, Peter, A. K. BEHRENSMEYER, & Robert T. BAKKER. 1980a. Taphonomy of the Morrison Formation (Kimmeridgian-Portlandian) and Cloverly Formation (Aptian-Albian) of the western United States. *Mem. Soc. Geol. France,* n.s., 139:87-93.

DODSON, Peter, A. K. BEHRENSMEYER, Robert T. BAKKER, & John S. McINTOSH. 1980b. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. *Paleobiology,* 6(2):208-232.

DODSON, Peter, Robert T. BAKKER, & Anna K. BEHRENSMEYER. 1983. Paleoecology of the dinosaur-bearing Morrison Formation. *Natl. Geographic Soc. Research Repts.,* 15: 145-156.

FARLOW, James O. 1976. Speculations about the diet and foraging behavior of large carnivorous dinosaurs. *Am. Midland Naturalist,* 95(1):186-191.

FISHER, Cassius A. 1909. *Geology of the Great Falls coal field, Montana.* U.S. Geol. Survey Bull. 356, pp. 1-85.

Fontaine, William M. 1905. Notes on some lower Cretaceous (Kootanie) plants from Montana. *In:* Lester F. Ward, *Status of the Mesozoic floras of the United States.* U.S. Geol. Survey Mon.

GALTON, Peter M., & James A. JENSEN. 1979. Remains of ornithopod dinosaurs from the lower Cretaceous of North America. *Brigham Young Univ. Geology Studies,* 25(3):1-10.

HAUN, John D. & James A. BARLOW, Jr. 1962. Lower Cretaceous stratigraphy of Wyoming. *Wyoming Geol. Assoc. Guidebook,* pp. 15-22.

HUGHES, Norman F. 1977. Paleo-succession of earliest angiosperm evolution. *Botanical Review,* 43(1):105-127.

JENKINS, Farish A., Jr. & A. W. CROMPTON. 1979. Triconodonta. *In:* J. A. Lilligraven, Z. Kielan-Jaworowska, & W. A. Clemens, eds., *Mesozoic mammals: the first two-thirds of mammalian history.* Berkeley: Univ. California Press.

JORDAN, Teresa E. 1981. Thrust loads and foreland basin evolution, Cretaceous, western United States. *Am. Assoc. Petroleum Geologists Bull.,* 65(12):2506-2520.

KNOWLTON, F. H. 1907. Description of a collection of Kootanie plants from the Great Falls coal field of Montana. *Smithsonian Misc. Coll.,* 50:105-128.

LAMMERS, Edward C. H. 1939. The origin and correlation of the Cloverly Conglomerate. *Jour. Geology,* 26(2):113-132.

LANGSTON, Wann, Jr. 1974. Nonmammalian Comanchean tetrapods. *Geoscience and Man,* 8:77-102.

MacFARLANE, M. J. 1976. *Laterite and landscape.* London: Academic Press.

MacKENZIE, David B. & David M. POOLE. 1962. Provenance of Dakota Group sandstones of the Western Interior. *Wyoming Geol. Assoc. Guidebook, 17th Ann. Field Conf.,* pp. 62-71.

MacKENZIE, Frederick T. & J. Donald RYAN. 1962. Cloverly-Lakota and Fall River paleocurrents in the Wyoming Rockies. *Wyoming Geol. Assoc. Guidebook, 17th Ann. Field Conf.,* pp. 44-61.

McGOOKEY, Donald P. 1972. The Cretaceous System. *In: Geologic atlas of the Rocky Mountain region.* Denver: Rocky Mountain Assoc. Geologists.

MIRSKY, Arthur. 1961. Mechanical analysis and heavy minerals, Morrison and Cloverly Formations, southern Big Horn Mountains, Wyoming. *Jour. Sedimentary Petrology,* 31(4): 571-585.

MOBERLY, Ralph, Jr. 1960. Morrison, Cloverly, and Sykes Mountain Formations, northern Bighorn Basin, Wyoming and Montana. *Geol. Soc. America Bull.,* 71:1137-1176.

————. 1962. Lower Cretaceous history of the Bighorn Basin, Wyoming. *Wyoming Geol. Assoc. Guidebook, 17th Ann. Field Conf.,* pp. 94-101.

OLLIER, C. D. 1967. A two-cycle theory of tropical pedology. *In:* J. V. Drew, ed., *Selected papers in soil formation and classification.* SSSA Spec. Pub. Ser., no. 1, Soil Soc. America, Inc., Madison.

OSTROM, John H. 1969. *Osteology of* Deinonychus antirrhopus, *an unusual theropod from the lower Cretaceous of Montana.* Peabody Mus. Natural History Bull. 30.

————. 1970. *Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana.* Peabody Mus. Natural History Bull. 35.

PECK, Raymond E. 1951. Nonmarine ostracodes--the subfamily Cyprideinae in the Rocky Mountain area. *Jour. Paleontology,* 25(3):307-320.

PECK, Raymond E. & William W. CRAIG. 1962. Lower Cretaceous nonmarine astracodes and charophytes of Wyoming and adjacent areas. *Wyoming Geol. Assoc. Guidebook,* pp. 33-43.

PECK, Raymond E. & Carl C. REKER. 1948. The Morrison and Cloverly Formations. *Wyoming Geol. Assoc. Guidebook,* pp. 125-139.

PRESCOTT, J. A. & R. L. PENDLETON. 1952. *Laterite and lateritic soils.* Commonwealth Agric. Bureaux, Farnham Royal, Bucks, England. Leicester: Geo. Gibbons, Ltd.

REESIDE, John B., Jr. 1957. Paleoecology of the Cretaceous seas of the Western Interior of the United States. *Geol. Soc. America Mem. 67,* pp. 505-542.

RETALLACK, Greg J. 1983. A paleopedological approach to the interpretation of terrestrial sedimentary rocks: the mid-Tertiary fossil soils of Badlands National Park, South Dakota. *Geol. Soc. America Bull.,* 94:823-840.

SHERMAN, G. Donald. 1951. The genesis and morphology of the alumina-rich laterite clays. *In: Problems of clay and laterite genesis.* Symp. Ann. Meeting of the Am. Inst. Mineralogical and Metallurgical Engineers.

SINGH, Chaitanya. 1975. Stratigraphic significance of early angiosperm pollen in the mid-Cretaceous strata of Alberta. *Geol. Assoc. Canada Spec. Paper 13,* pp. 365-389.

SUES, Hans-Dieter. 1980. Anatomy and relationships of a new hypsilophodontid dinosaur from the lower Cretaceous of North America. *Palaeontographica,* 169:51-72.

TAYLOR, Thomas N. 1981. *Paleobotany: An introduction to fossil plant biology.* New York: McGraw-Hill Book Co.

WARD, Lester F. 1905. *Status of the Mesozoic floras of the United States.* U.S. Geol. Survey Mon.

WEAVER, Charles E. & Lin D. POLLARD. 1973. *The chemistry of clay minerals.* Developments in sedimentology 15. New York: Elsevier Pub. Co.

WEISHAMPEL, David B. 1981. *The evolution of ornithopod jaw mechanics.* Unpub. Ph.D. dissert., Univ. Pennsylvania.

WEISHAMPEL, David B. & Judith B. WEISHAMPEL. 1983. Annotated localities of ornithopod dinosaurs: implications to Mesozoic paleobiogeography. *The Mosasaur,* 1:43-87.

WEISHAMPEL, David B. 1984. Interactions between Mesozoic plants and vertebrates: fructifications and seed predation. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* 167(2):224-250.

YEN, Teng-Chien. 1949. Review of the lower Cretaceous fresh-water molluscan faunas of North America. *Jour. Paleontology,* 23(5):465-470.

YOUNG, Robert G. 1970. Lower Cretaceous of Wyoming and the southern Rockies. *Wyoming Geol. Assoc. Guidebook, 22nd Ann. Field Conf.,* pp. 147-159.